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# PLACE-CONSTANTS FOR ASTER PRENANTHOIDES

A DISSERTATION

SUBMITTED TO THE FACULTY OF THE OGDEN GRADUATE SCHOOL OF  
SCIENCE, IN CANDIDACY FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY


(DEPARTMENT OF BOTANY)

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BY  
GEORGE HARRISON SHULL

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CHICAGO  
1904



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PLACE-CONSTANTS FOR ASTER PRENANTHOIDES.  
CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.  
LXIV.

GEORGE HARRISON SHULL.

(WITH EIGHTEEN FIGURES)

I. INTRODUCTION.

GEOGRAPHIC isolation has long been accredited as an important factor in the process of evolution, but with the introduction of methods calculated to demonstrate the evolutionary processes an altogether new conception has been gained regarding the importance of locality as a modifying factor. Statistical methods have shown that the organisms of any species from different stations, often quite near each other, are not to be considered homogeneous, and that in order to establish a proper basis for comparison investigations must deal with definite areas. The modal condition of any species prevailing on such a limited area is known as a "place-mode" for that species at that place.

The importance of determining and recording place-modes for various species was first emphasized by DAVENPORT (1899a), and in response to his appeal a considerable number of local statistical studies have been made. Some of these studies have shown that the determination of place-constants is not so simple a problem as was at first supposed. As a result of my earlier studies on *Aster* (SHULL 1902) it was shown that the establishment of place-constants for a species of *Aster* would involve the collection of all the heads produced during the season, since there is a continuous and more or less regular change in the variable characters from day to day throughout the season. It was suggested there that considerable differences might also be presented by the same population from season to season. The results of a number of studies on various species by other investigators, both before and since my study of *Aster*, either lead to the same conclusion or admit of the same explanation (BURKILL 1895, MACLEOD 1899, LUDWIG 1901, TOWER 1902, YULE 1902, PEARSON 1903, REINÖHL 1903, etc.).

TOWER (1902) discusses the bearing of these results upon the establishment of place-constants, and concludes "that the 'place-mode' for a species or for a character of a species should represent the average prevailing condition at a given place during a period of observation continued through years or long enough to eliminate the effect of secular fluctuations."<sup>1</sup>

It has been proved conclusively that conditions of variability which are a function of place are masked by others associated with time, and before we can satisfactorily arrive at the one the other must be eliminated. In the efforts which have thus far been made to establish place-constants this fact has not been taken into account. Indeed, we do not yet know how to take it into account, since no adequate investigation has been made of changes in variability which take place during the season and from season to season. It was to add to our knowledge of such secular variation and to contribute by its elimination to the establishment of true place-constants that the present study was undertaken.

<sup>1</sup> In his summary TOWER gives the following definition: "A 'place-mode' is the average prevailing state of a homogeneous lot of individuals [*i. e.*, of the same pleomorphic condition and stage of development] characteristic of a particular place and season, as determined by observations carried on long enough to eliminate the effects of secular climatic fluctuations." The limitation of a place-mode to a *particular season* was plainly unintentional, as it is inconsistent with the requirement that the observations be carried on long enough to eliminate the effects of secular climatic fluctuations.

PEARSON (1902) objects to this definition as not being biometric. He says: "It might refer to any constant whatever of the frequency—to the mean, the mode, the variability, or indeed to the whole frequency distribution itself." TOWER's application of the term place-mode to the *average prevailing condition* of a homogeneous population is in harmony with a well-known philological principle which has wrested very many words from their original signification to meanings of greater or less inclusiveness, because the original concept as limited by the literal meaning of the symbol used proved to be of comparatively little importance. In very many instances the *mode* is the least important constant involved, and in others—particularly in the variation of plants—the theoretical mode is at present indeterminable. As no one thought, in studying place-modes, of limiting his studies to the theoretical *mode*, it was not unnatural so to extend the meaning of place-mode as to involve all the quantitative relations of a population.

While it was evidently DAVENPORT's intention in proposing the word "place-mode" to use it in its strict mathematical sense, a reference to his definition will show how easy it was to make it include the entire condition of the population. He says (1899a): "I use the word 'place-mode' to embody a well-known idea, namely that a

## II. MATERIAL AND METHODS.

This study is based upon the flowering heads of *Aster prenanthoides* Muhl. collected thrice a week from the same area which furnished the serial collections for my earlier studies (SHULL 1902). This species is in some ways an ideal subject for studies of this kind. The heads are beautifully regular, as may be seen in *fig. 1*. They are little subject to injuries, and almost the only heads which must be thrown away are those in which insect larvae have hatched and subsisted upon the developing flowers. Such cases are not numerous, amounting to less than 2 per cent. of the heads collected this year.

The personal equation was eliminated in the same manner as in my former work, *i. e.*, by the collection of every head that bloomed on a naturally circumscribed area. The method used in making the counts was also the same, the heads being completely dissected. This method prevents the errors which will frequently occur in the counting of rays without complete dissection—errors

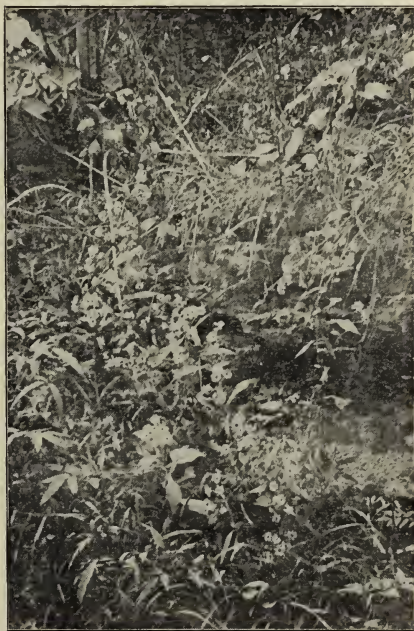


FIG. 1.—*Aster prenanthoides* at Clifton, Ohio.

species has a different *mode* (*i. e.*, a different *prevailing* condition of size, color, etc. in different localities. The person who seeks to determine a place-mode determines the prevailing dimension of the principal measurable qualities (and practically all qualities of organisms are measurable) of a species as it occurs in the locality in question."

It seems desirable in applying the exact methods of the mathematician to biology to retain the exact mathematical significance of the word "place-mode," though the term then becomes of comparatively little usefulness. As a more inclusive term, involving the characteristics of any or all the measurable qualities of a species as represented by a lot of individuals occurring at any place in question, let us adopt the word *place-condition* or *place-habit*. We may then say that we investigate the place-habit or place-condition of a species at a particular place in order to determine or establish the place-constants, among these being the place-mode.



resulting from the loss of rays due to age or other causes—and it saves the necessity of discarding any material on this ground, since the remains of the ray-flowers are always distinguishable from the disk-flowers when they are separated.

It ought not to be necessary in work of this kind to give assurance that no material has been arbitrarily discarded, either in collection or in seriation, but the importance of this matter seems to be too little appreciated. If one student arbitrarily discards material, who else in working over the same material will arbitrarily discard on the same basis? And if an investigation cannot be repeated by another investigator with at least approximately identical results, of what value is it? TOWER (1902) assumed that his failure to get a mode at 34 in *Chrysanthemum Leucanthemum* might be due to the fact that he discarded a number of heads on account of age. He states that counts of some of this rejected material showed that all of the heads had a large number of rays. What would have been the result had he counted all the heads he rejected? Miss SMALLWOOD (1903) "arbitrarily threw out the small" specimens of beach-flea and then presented statistics as to the size and variability of the remainder, as if these data could have either interest or scientific value.<sup>2</sup> If anomalies appear when all the data are seriated, they should be explained if possible, but explained or unexplained the data should be given, because these have value whether the explanation has or not.

In calculating the various constants I have again used the formulae tabulated in DAVENPORT'S (1899b) *Statistical methods*, except that instead of DUNCKER'S method of calculating the coefficient of correlation I have used the neat method adopted by YULE (1897), which may be expressed by the formula

$$\rho = \left( \frac{\sum jx'x''}{n} - v_1' v_1'' \right) \frac{1}{\sigma' \sigma''},$$

in which  $x'$  and  $x''$  are the deviations from an integral assumed mean of subject and relative classes respectively,  $j$  is the frequency of occurrence of each combination of subject and relative deviations,

<sup>2</sup> In justice to Miss SMALLWOOD it should be said that her paper deals chiefly with the ethological relations of the beach-flea, and that she seems to have appreciated the unsatisfactory character of her quantitative results.

$n$  is the whole number of variates,  $\nu_i'$  and  $\nu_i''$  are the deviations of the assumed means from the true means, and  $\sigma'$  and  $\sigma''$  the errors of mean square or "standard deviations" respectively of the subject and relative categories.<sup>3</sup>

### III. LOCALITY AND HABITAT.

Flowers collected from the hillsides differ in a marked way from those of the same species collected in the lowlands of the same locality, as has been shown in many instances by DE VRIES, LUDWIG, REINÖHL, and others. This is a question of habitat. It remains an unsolved problem whether plants are not so sensitive to edaphic and local climatic conditions as to make impossible the derivation by statistical methods of anything more fundamental than the fact and the degree of this extreme sensitiveness. This problem can be solved only by long and carefully conducted investigations. In order that we may discriminate between the influences of habitat and locality in making studies in variation, it becomes necessary to record as carefully as possible the habitat in which the material has been collected, and so to indicate the locality that future investigators may visit the identical area studied.

The definite character both of habitat and of locality has strongly commended the choice of this particular area of *Aster prenanthoides* for such thorough investigation as is needed to elucidate the complex problems involved in work of this kind.

Clifton is a small village on the boundary between Clark and Greene counties, Ohio, in lat.  $39^{\circ} 48' 43''$  north and long.  $83^{\circ} 48' 41''$  west. The Little Miami River, on whose northern bank the village lies, occupies a post-glacial channel in massive gray Niagara limestone, forming a deep and narrow gorge widely known for the beauty of its scenery. About one kilometer west of the village two small streams enter the river from the north. Both of these tributary streams have cut gorges in the limestone, but, being unable to corrade their beds so rapidly as does the river, they have been left high above the level of the river in hanging valleys. At about 10–20 m from the river the Yellow Springs turnpike crosses these streams by two stone arches. The area chosen as the source of material for this study is

<sup>3</sup> This method displaces DUNCKER's method in the second edition of DAVENPORT's *Statistical methods* which has just appeared.

that portion of the more westerly tributary ravine lying between the road and the precipice over which the stream falls into the river. The locality is indicated by a star on the map (fig. 2).

An important theoretical consideration is the relation of the locality to the whole range of the species and to the direction of its migration.

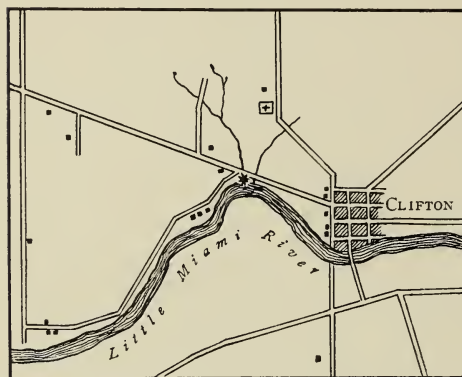


FIG. 2.—Map of Clifton and vicinity; station for *Aster prenanthoides* marked with a star.

What relation does the variability of a species near its limit of range bear to that at its center? Is there a progressive change of variable characters along the lines of migration radiating from the center of distribution of the species? ADAMS (1902) accepts such progressive change as one of his ten criteria for the determination of centers of distribution. He concludes that the

southeastern United States has been the principal center of post-glacial distribution for the eastern half of North America. The determination of place-constants in various parts of the range would test the value of this criterion. It is to be hoped that investigators in other places will make studies similar to this for the purpose of throwing a more certain light on these principles.

To show the relation of Clifton, Ohio, to the total range of *Aster prenanthoides* I present in fig. 3 a map showing the range of the species as represented at the present time by specimens in the leading American herbaria. Such a map is always to some extent a commentary on the limitations of the herbaria, and does not correctly represent the relative frequency of the species in the different parts of its range. E. S. BURGESS, the well-known specialist on the genus *Aster*, writes that the stations in the Berkeley Hills, Mass., and in the Catskills and Shawangunk Mountains, N. Y., are really extralimital, "the species becoming common 300 miles [480 km] westward, and reaching proper development along the southern shore of Lake Erie and thence through western Pennsylvania." The fewness of



the stations in the western half of the range is due to the general scarcity of herbarium material from this area rather than to the rarity of the species. It will be seen from this map that the Clifton station (marked with a star) is very nearly central.

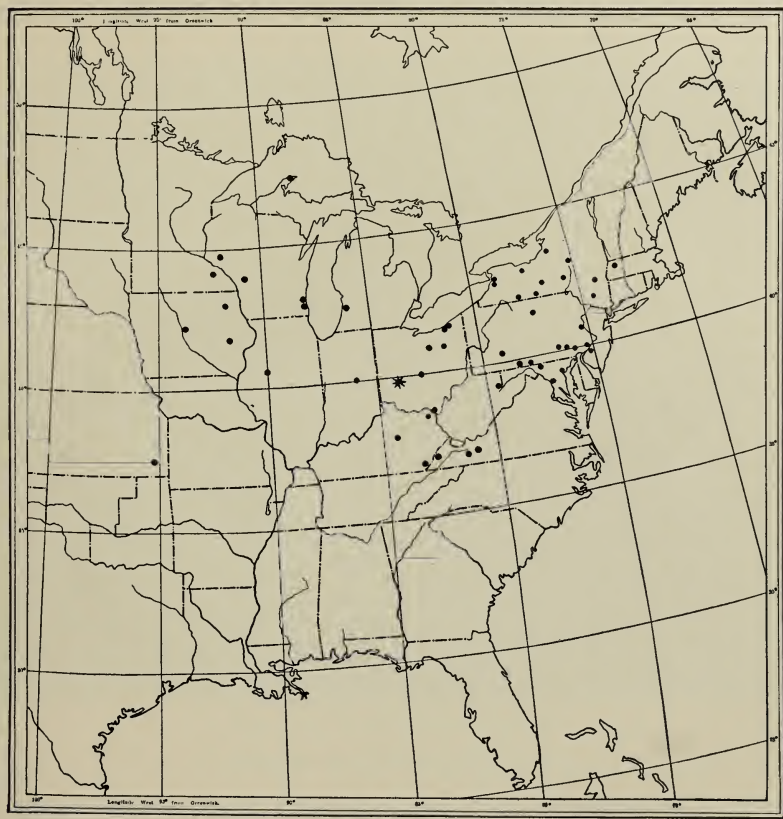


FIG. 3.—The range of *Aster prenanthoides* as represented by specimens in the leading American herbaria;<sup>4</sup> Clifton, Ohio, marked with a star.

<sup>4</sup> The stations represented on the map are as follows: MASSACHUSETTS: Berkeley Hills. NEW YORK: Chenango Co., Oswego Co., Tompkins Co., Andover, Big Tree, Bridgewater, Buffalo, Elmira, Macedon, Catskill Mts., Shawangunk Mts. NEW JERSEY: Woodbury. PENNSYLVANIA: Bedford Co., Chester Co., Conewago Co., Lancaster Co., Westmoreland Co., Easton, Mercersburg, Philadelphia, Trout Run. MARYLAND: Baltimore, Emmittsburg. DISTRICT OF COLUMBIA: Washington. VIRGINIA: Big Stone Gap, Pulaski, Wytheville. WEST VIRGINIA: Aurora. KENTUCKY:

The habitat of the population in question is typical of the species, if we may judge from the statements made in the various manuals, all of which agree that the characteristic habitat is along margins of streams in shady places. This fact will make it easy to find these plants growing under essentially the same conditions in other localities, and thus facilitate the establishment of place-constants which shall be



FIG. 4.—The habitat, looking south.

properly comparable. The general character of the habitat at Clifton will be best understood by a reference to *figs. 1, 4, and 5*. It will be at once recognized that we have here an example of temporary mesophytic climax characteristic of young ravines, the luxuriance of vegeta-

Bell Co., Carter Co., Lexington. OHIO: Franklin Co., Berea, Cleveland, Clifton, Ironton, Mansfield, Wooster. INDIANA: Hamilton Co. ILLINOIS: Canton. MICHIGAN: Allegan Co., Keweenaw Co. WISCONSIN: Eau Galle, Milwaukee, Racine, Sparta. MINNESOTA: Mazeppa. IOWA: Fayette Co., Johnson Co., Ames. KANSAS: Neosho Co.

tion being due to the moderation of extremes of temperature, light, etc., the protection from winds, and the consequent maintenance of a relatively high degree of humidity. Besides the relative constancy of atmospheric conditions, it should be noted that the stream which occupies the ravine, and along whose margin the *Aster prenanthoides* is growing, is a permanent, spring-fed stream draining so small an



FIG. 5.—The habitat, looking north.

area as to be little subject to fluctuations due to the alternations of dry and rainy periods. The map shown in *fig. 6* accurately represents the present position of the stream and the location of the areas of *Aster prenanthoides* with reference to it, thus enabling the future investigator to note any changes of area or relation which might have an influence upon the variability.

#### IV. RESULTS.

The collections having been made about three times a week, regardless of the number of heads which were in bloom at any time, it does not seem desirable to present curves and correlation tables



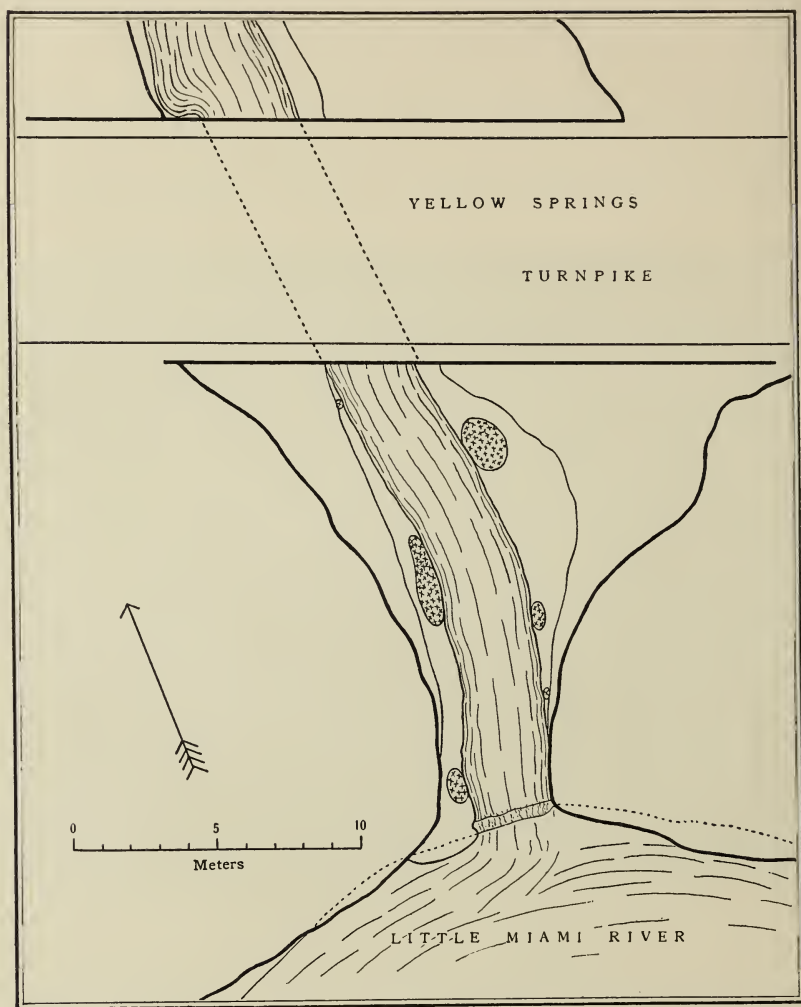


FIG. 6.—Map showing the relation of *Aster prenanthoides* to the stream at the Clifton station; heavy contours represent the upper margin of the cliffs; light contours show the limit of the flood plains; depth of ravine 5–7 m; height of hanging valley above river level 7–8 m.

of each separate collection. In order to make the original data available for any purpose to which other students may wish to turn it, I give in tabulated form the results of the several collections (Tables A, B, and C).

TABLE A.

BRACIS.

No.	SEPTEMBER, 1903										OCTOBER, 1903			TOTAL 1903	1900 IN %	1903 IN %	SUM IN %
	12	14	16	18	21	23	25	28	30	2	6	9					
18	..	..	..	..	..	..	I	..	..	..	..	..	I	....	.13	.07	
19	..	..	..	..	..	..	..	..	..	..	..	..	0	....	.00	.00	
20	..	..	..	..	..	..	..	..	..	..	I	..	I	....	.13	.07	
21	..	..	..	..	..	..	..	..	I	..	..	..	I	....	.13	.07	
22	..	..	..	..	I	..	I	..	..	I	..	..	3	....	.40	.21	
23	..	..	..	I	..	..	I	2	..	..	..	..	4	....	.53	.28	
24	I	..	..	..	I	..	I	2	..	..	..	..	5	....	.66	.35	
25	I	..	I	..	I	I	..	..	I	..	I	..	6	....	.79	.42	
26	2	..	..	I	I	I	..	I	2	..	I	..	9	....	1.19	.64	
27	..	..	..	..	..	2	..	2	..	I	5	..	10	....	1.32	.71	
28	2	I	..	..	3	I	..	..	I	6	7	..	21	....	2.77	1.48	
29	5	..	..	I	I	I	I	3	4	5	9	..	30	.30	3.96	2.26	
30	4	2	..	I	..	..	2	6	4	5	6	..	30	.46	3.96	2.33	
31	3	2	..	I	..	I	..	5	3	9	4	..	28	.15	3.70	2.05	
32	2	I	..	2	3	4	..	9	2	6	7	..	36	1.22	4.75	3.11	
33	I	..	..	..	..	3	2	10	4	5	10	2	37	.76	4.88	2.97	
34	2	I	..	I	5	4	6	8	2	7	6	..	42	2.43	5.54	4.10	
35	..	2	I	3	2	6	..	4	7	4	4	..	33	.91	4.36	2.76	
36	..	..	..	5	2	5	3	6	6	5	I	..	33	2.28	4.36	3.39	
37	..	..	I	I	I	I	4	10	4	I	6	..	29	3.50	3.83	3.68	
38	..	I	2	3	4	5	2	5	5	4	3	I	35	3.65	4.62	4.17	
39	I	I	3	6	..	4	3	7	4	4	4	I	38	5.62	5.02	5.30	
40	..	..	I	I	2	3	2	3	3	5	2	..	22	5.47	2.90	4.10	
41	..	2	2	3	4	6	5	5	3	I	..	..	31	7.30	4.09	5.59	
42	I	2	I	4	I	3	3	5	I	6	I	..	28	5.17	3.70	4.38	
43	..	I	..	2	4	9	4	6	..	I	..	..	27	7.14	3.56	5.30	
44	..	2	I	2	I	8	3	I	I	3	..	..	22	6.99	2.90	4.81	
45	..	2	I	3	I	3	7	5	..	..	I	..	23	6.54	3.04	4.67	
46	..	..	I	6	2	5	3	7	I	..	2	..	27	5.02	3.56	4.24	
47	I	3	..	9	2	3	2	3	..	..	I	..	24	5.32	3.17	4.17	
48	2	2	..	6	2	2	2	3	..	I	I	..	21	5.62	2.77	4.10	
49	I	4	4	6	5	2	5	..	I	2	..	..	30	6.99	3.96	5.37	
50	3	4	I	2	5	I	..	..	..	I	..	..	17	6.23	2.24	4.10	
51	..	..	2	8	3	I	I	3	I	..	..	..	19	3.04	2.51	2.76	
52	2	I	..	4	I	3	..	..	3	..	..	..	14	2.74	1.85	2.26	
53	I	I	..	5	2	2	..	2	..	..	..	..	13	1.98	1.72	1.84	
54	..	I	..	I	..	I	..	..	..	..	..	..	3	1.37	.40	.85	
55	..	..	..	..	..	..	..	..	..	..	..	..	0	.30	.00	.14	
56	I	..	I	..	..	..	..	..	..	..	..	..	2	.15	.26	.21	
57	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
58	..	..	..	..	..	..	..	..	..	..	..	..	0	.15	.00	.07	
59	..	..	..	..	..	..	..	..	..	..	..	..	0	.46	.00	.21	
60	..	I	..	..	..	..	..	..	..	..	..	..	I	.30	.13	.21	
61	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
62	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
63	..	..	..	..	..	I	..	..	..	..	..	..	I	.15	.13	.14	
64	..	..	..	..	..	..	..	..	..	..	..	..	..	.15	....	.07	
	36	37	23	88	60	92	64	123	64	83	83	4	757				



TABLE B.

RAYS.

No.	SEPTEMBER, 1903										OCTOBER, 1903			TOTAL 1903	1900 IN %	1903 IN %	SUM IN %
	12	14	16	18	21	23	25	28	30	2	6	9					
12	..	..	..	..	..	..	..	I	..	I	..	..	2	....	.26	.11	
13	..	..	..	I	..	..	..	..	..	..	..	..	I	....	.13	.07	
14	..	..	..	..	..	..	I	..	I	..	2	..	4	....	.53	.28	
15	..	..	..	I	I	..	..	..	..	..	I	..	3	....	.40	.21	
16	4	..	I	I	..	2	3	2	I	I	I	..	16	....	2.11	1.13	
17	2	I	..	..	..	..	..	2	..	..	3	..	8	.15	1.06	.64	
18	5	..	..	I	3	I	..	3	3	2	3	..	21	.00	2.77	1.48	
19	I	2	..	..	4	3	..	5	..	4	10	..	29	.91	3.83	2.47	
20	7	I	..	I	I	3	I	12	4	4	7	..	41	.91	5.41	3.32	
21	2	2	..	3	5	7	3	9	6	7	9	..	53	2.13	7.00	4.74	
22	I	2	I	4	3	11	5	13	8	15	11	..	74	5.12	9.77	7.56	
23	I	I	5	5	3	8	5	12	6	7	6	2	61	5.32	8.05	6.79	
24	..	I	2	7	4	4	3	4	7	8	6	..	46	7.30	6.07	6.65	
25	I	2	2	2	2	5	5	10	6	9	8	I	53	7.45	7.00	7.21	
26	I	2	2	3	5	2	8	14	9	5	6	..	57	8.66	7.52	8.06	
27	..	I	2	4	4	7	5	11	3	5	4	I	47	8.97	6.20	7.49	
28	I	8	I	2	..	6	6	6	4	5	2	..	41	8.36	5.41	6.79	
29	I	I	..	6	5	11	3	6	I	2	I	..	37	7.14	4.88	5.94	
30	..	4	..	4	3	6	4	4	I	4	2	..	32	7.14	4.22	5.59	
31	I	2	3	8	I	3	5	4	I	4	..	..	32	7.90	4.22	5.94	
32	5	..	I	8	2	2	2	3	2	..	..	..	25	6.23	3.30	4.67	
33	..	2	..	12	6	7	3	I	..	..	..	..	31	7.45	4.09	5.66	
34	..	I	I	8	2	3	..	I	..	..	..	..	16	5.02	2.11	3.46	
35	2	I	I	4	5	..	I	..	..	..	I	..	15	1.67	1.98	1.84	
36	I	2	I	2	I	I	..	..	..	..	..	..	8	1.22	1.06	1.13	
37	..	..	..	..	..	..	..	..	..	..	..	..	0	.15	.00	.07	
38	..	..	..	I	..	..	..	I	..	..	..	..	2	.46	.26	.35	
39	..	..	..	..	..	..	..	..	..	..	..	..	0	.15	.00	.07	
40	..	I	..	..	..	..	..	..	I	..	..	..	2	.15	.26	.21	
41	..	..	..	..	..	..	..	..	..	..	..	..	..	.00	....	.00	
42	..	..	..	..	..	..	..	..	..	..	..	..	..	.15	....	.07	
	36	37	23	88	60	92	64	123	64	83	83	4	757				

TABLE C.

DISK-FLORETS.

No.	SEPTEMBER, 1903										OCTOBER, 1903			TOTAL 1903	1900 IN %	1903 IN %	SUM IN %
	12	14	16	18	21	23	25	28	30	2	6	9					
14	..	..	..	..	..	..	..	..	I	..	..	..	I	....	.13	.07	
15	..	..	..	..	..	..	..	..	..	..	..	..	O	....	.00	.00	
16	..	..	..	..	..	..	I	..	..	..	..	..	I	....	.13	.07	
17	..	..	..	I	..	..	..	..	..	..	..	..	I	....	.13	.07	
18	..	..	I	..	..	..	..	I	..	..	..	..	2	....	.26	.14	
19	..	..	..	..	..	..	..	..	..	..	..	..	O	....	.00	.00	
20	I	..	..	..	..	..	..	..	..	I	..	..	2	....	.26	.14	
21	..	..	..	..	..	..	..	..	..	..	I	..	I	....	.13	.07	
22	..	..	..	..	..	..	..	..	..	..	..	..	O	....	.00	.00	
23	..	..	..	..	..	..	I	..	..	..	I	..	2	....	.26	.14	
24	..	..	..	..	..	..	..	..	I	..	..	..	I	....	.13	.07	
25	..	..	..	..	..	..	..	..	I	..	I	..	2	.15	.26	.21	

TABLE C (continued).

No.	SEPTEMBER, 1903										OCTOBER, 1903			TOTAL 1903	1900 IN %	1903 IN %	SUM IN %
	12	14	16	18	21	23	25	28	30	2	6	9					
21	..	..	..	..	..	..	I	..	2	..	I	..	4	.00	.53	.28	
27	..	..	..	..	..	I	..	2	..	I	..	..	4	.00	.53	.28	
28	I	..	..	..	2	..	..	I	..	..	3	..	7	.00	.92	.49	
29	I	..	..	..	..	2	..	..	I	I	4	..	9	.00	1.10	.64	
30	3	..	..	..	I	..	..	..	..	I	5	..	10	.00	1.32	.71	
31	2	..	..	..	2	I	I	3	..	I	I	..	11	.15	1.45	.85	
32	..	..	..	..	2	3	I	3	..	..	I	..	10	.15	1.32	.78	
33	I	I	..	..	I	..	..	2	..	5	2	..	12	.15	1.58	.92	
34	I	..	..	4	..	2	..	I	3	I	3	..	15	.46	1.98	1.27	
35	3	I	..	I	I	2	I	5	2	4	9	I	30	.15	3.96	2.19	
36	..	I	..	2	I	2	I	4	I	4	5	..	21	.00	2.77	1.48	
37	2	..	2	I	5	2	I	4	3	3	6	..	29	.46	3.83	2.26	
38	3	..	..	2	I	I	3	4	3	6	4	..	27	.46	3.56	2.12	
39	2	3	3	I	I	3	3	5	3	5	I	..	30	.61	3.96	2.40	
40	2	I	..	2	2	2	I	5	..	4	4	..	23	1.98	3.04	2.55	
41	I	..	..	2	I	2	2	8	3	4	5	2	30	1.22	3.96	2.60	
42	..	2	I	4	..	5	2	9	4	6	3	..	36	2.28	4.75	3.61	
43	2	I	..	2	I	4	..	6	2	2	2	..	22	4.10	2.90	3.46	
44	..	..	..	..	I	5	I	6	6	2	4	I	26	3.50	3.43	3.46	
45	..	I	4	3	2	4	3	3	7	4	4	..	35	5.78	4.62	5.16	
46	..	2	I	I	2	2	2	5	I	9	I	..	26	6.54	3.43	4.88	
47	2	3	2	2	3	3	2	4	2	7	2	..	32	5.32	4.22	4.74	
48	..	..	..	3	..	7	2	4	6	2	I	..	25	5.93	3.30	4.52	
49	..	3	..	3	3	I	2	5	2	4	2	..	25	7.14	3.30	5.00	
50	..	I	2	I	2	2	3	9	4	3	4	..	31	7.14	4.09	5.51	
51	..	I	I	5	2	4	2	3	I	..	I	..	20	5.47	2.64	3.96	
52	I	I	..	4	..	4	I	5	2	..	I	..	19	6.84	2.51	4.52	
53	..	I	I	3	2	2	4	5	..	3	..	..	21	6.38	2.77	4.45	
54	..	..	..	2	I	4	5	2	I	..	I	..	16	4.86	2.11	3.39	
55	I	3	..	2	4	3	5	5	..	..	..	..	23	3.95	3.04	3.46	
56	I	3	I	4	6	3	3	2	..	..	..	..	23	4.56	3.04	3.75	
57	..	..	..	3	3	8	2	I	I	..	..	..	18	2.74	2.38	2.55	
58	..	I	2	6	2	I	4	I	I	..	..	..	18	2.13	2.38	2.26	
59	2	..	I	5	I	4	2	..	..	..	..	..	15	1.67	1.98	1.84	
60	I	I	..	4	3	I	..	..	..	..	..	..	10	2.13	1.32	1.70	
61	I	..	..	2	..	I	..	..	..	..	..	..	4	1.37	.53	.92	
62	..	..	..	3	I	..	I	..	..	..	..	..	5	1.22	.66	.92	
63	..	..	..	..	..	I	..	..	..	..	..	..	I	.61	.13	.35	
64	2	..	I	2	I	..	I	..	..	..	..	..	7	.00	.92	.49	
65	..	..	..	I	..	..	..	..	..	..	..	..	I	1.06	.13	.57	
66	..	..	..	2	..	..	..	..	..	..	..	..	2	.46	.26	.35	
67	..	I	..	2	..	..	..	..	..	..	..	..	3	.00	.40	.21	
68	..	..	..	3	..	..	..	..	..	..	..	..	3	.30	.40	.35	
69	..	..	..	..	..	..	..	..	..	..	..	..	0	.15	.00	.07	
70	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
71	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
72	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
73	..	I	..	..	..	..	..	..	..	..	..	..	I	.15	.13	.14	
74	..	2	..	..	..	..	..	..	..	..	..	..	2	.15	.26	.21	
75	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
76	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
77	..	..	..	..	..	..	..	..	..	..	..	..	0	.00	.00	.00	
78	..	2	..	..	..	..	..	..	..	..	..	..	2	.00	.26	.14	
79	..	..	..	..	..	..	..	..	..	..	..	..	..	.15	....	.07	
	36	37	23	88	60	92	64	123	64	83	83	4	757				

TABLE D.  
CHIEF CONSTANTS OF THE SEVERAL COLLECTIONS.

Bracts	Sep. 12	Sep. 14	Sep. 16	Sep. 18	Sep. 21	Sep. 23	Sep. 25	Sep. 28	Sep. 30	Oct. 2	Oct. 6	Oct. 9
Mean.....	36.555	43.297	43.174	43.898	40.700	40.652	39.828	37.423	36.016	35.120	33.006	35.750
P. E. M.....	± 1.110	± .868	± .947	± .500	± .723	± .492	± .598	± .401	± .543	± .423	± .389	± .935
σ.....	9.870	7.829	6.735	6.951	8.303	7.002	7.090	6.598	6.438	5.717	5.247	2.773
P. E. σ.....	± .785	± .614	± .670	± .353	± .511	± .348	± .423	± .284	± .384	± .299	± .275	± .661
C. V.....	27.000	18.081	15.600	15.835	20.401	17.225	17.801	17.630	17.877	16.278	15.854	7.756
P. E. v.....	± 2.146	± 1.418	± 1.551	± .805	± 1.256	± .857	± 1.061	± .758	± 1.066	± .852	± .830	± 1.849

#### Rays

	Sep. 12	Sep. 14	Sep. 16	Sep. 18	Sep. 21	Sep. 23	Sep. 25	Sep. 28	Sep. 30	Oct. 2	Oct. 6	Oct. 9
Mean.....	23.305	27.540	26.739	28.681	26.600	26.033	26.187	24.179	24.109	23.880	22.301	24.500
P. E. M.....	± .720	± .582	± .669	± .380	± .485	± .326	± .392	± .249	± .342	± .272	± .278	± .559
σ.....	6.407	5.248	4.757	5.284	5.571	4.628	4.650	4.092	4.058	3.668	3.757	1.658
P. E. σ.....	± .509	± .412	± .473	± .269	± .343	± .230	± .277	± .176	± .242	± .192	± .107	± .396
C. V.....	27.490	19.158	17.790	18.423	20.945	17.780	17.756	16.926	16.834	15.361	16.846	6.769
P. E. v.....	± 2.185	± 1.494	± 1.769	± .937	± 1.290	± .884	± 1.059	± .728	± 1.004	± .804	± .882	± 1.614

#### Disk-florets

	Sep. 12	Sep. 14	Sep. 16	Sep. 18	Sep. 21	Sep. 23	Sep. 25	Sep. 28	Sep. 30	Oct. 2	Oct. 6	Oct. 9
Mean.....	41.611	51.720	46.522	51.511	47.100	46.891	47.672	43.569	42.187	41.301	38.072	40.250
P. E. M.....	± 1.282	± 1.318	± 1.343	± .724	± .862	± .603	± .813	± .450	± .682	± .469	± .535	± 1.103
σ.....	11.405	11.884	9.546	10.062	9.899	8.569	9.647	7.539	8.087	6.339	7.219	3.269
P. E. σ.....	± .907	± .932	± .949	± .512	± .610	± .426	± .575	± .324	± .482	± .332	± .378	± .780
C. V.....	27.408	22.973	20.519	19.534	21.017	18.274	20.236	17.303	19.170	15.349	18.962	8.122
P. E. v.....	± 2.179	± 1.801	± 2.041	± .993	± 1.294	± .909	± 1.206	± .744	± 1.143	± .804	± .993	± 1.937

In Table D are given the more important constants of the several collections with the probable errors of the determination. The average deviation is omitted as having no significance, since the probable error of the determination is almost as large as the determined value of the constant. It will be noted on examining this table that all the constants are quite variable, and that only the mean seems to follow a rather definite law, beginning low, then leaping almost immediately to the maximum, after which there is a gradual fall until almost the end, when a slight rise appears. The fall of mean values from the maximum on September 18 to the minimum on October 6 was 24.6 per cent. in bracts, 22.25 per cent. in rays, and 26.4 per cent. in disk-florets. The changes of mean value for each set of variants from the beginning to the end of the flowering season and the corresponding changes observed in 1900 are shown graphically in *fig. 7*.

1. *Bracts*.—The frequency polygon for the bracts is shown in fig. 8. The mean value is  $38.597 \pm .189$ , and a number of empirical modes are present. Some, if not all, of these are doubtless due to the smallness of the number of heads counted. It will be noted

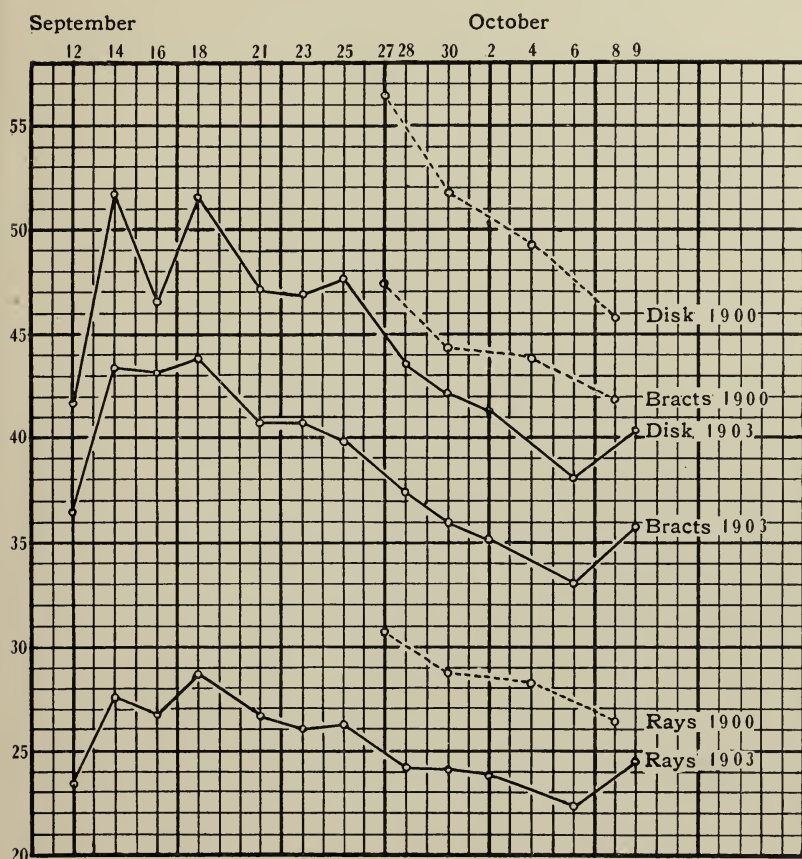


FIG. 7.—Curves showing the changes in the mean numbers of parts in the heads from the beginning to the end of the season, and the difference between the two collections, 1900 and 1903.

that the most prominent modes are those which lie below the mean value; *i. e.*, if one may speak of skewness in multimodal curves, there is evident here a strong positive skewness. The breadth of the curve exhibits to the eye the great variability, which may be expressed

numerically by the standard deviation  $7.692 \pm .133$ , or by the coefficient of variability  $19.928 \pm .345$ .

2. *Rays*.—The ray-curve shown in fig. 9 has the mean at  $25.247 \pm .122$  and by much the strongest mode at 22, so that here again there is a very prominent skewing of the curve. The empirical

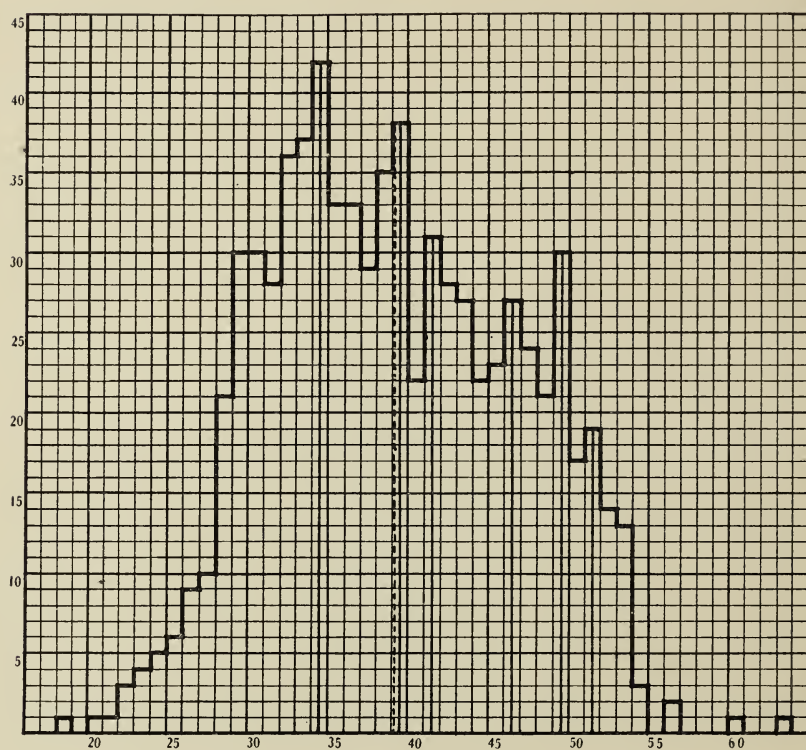


FIG. 8.—Bract-curve for 757 heads collected in 1903: mean  $38.597 \pm .189$ ; empirical modes 29-30, 34, 39, 41, 46, 49, 51;  $\sigma = 7.692 \pm .133$ .

modes at 16, 22, 26, 33 are somewhat suggestive of the series which LUDWIG, DE VRIES, and others have shown to be so common, but aside from such suggestion can have little meaning. The standard deviation  $4.990 \pm .087$  is considerably less than that of the bracts, while the coefficient of variability,  $19.764 \pm .344$ , is practically the same.



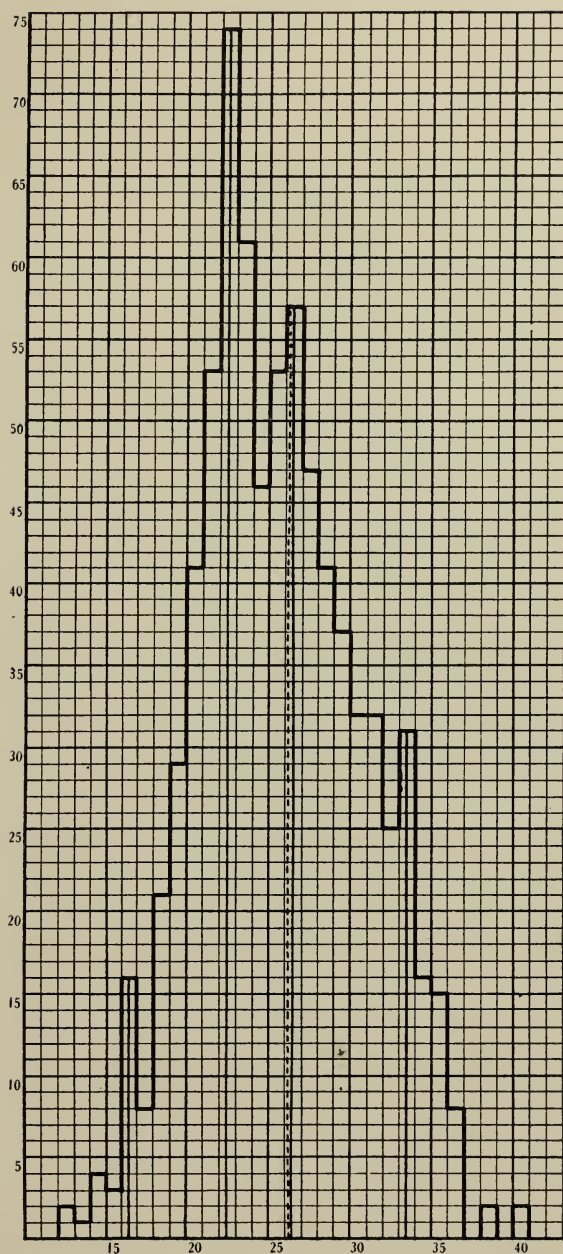


FIG. 9.—Ray-curve for 757 heads collected in 1903: mean  $25.247 \pm .122$ ; empirical modes 16, 22, 26, 33;  $\sigma = 4.9899 \pm .0865$ .

3. *Disk-florets*.—The polygon of distribution of the disk-florets is presented in *fig. 10*. The range, from 14 to 78, is so wide that 757 heads are quite insufficient to make the many empirical modes of any

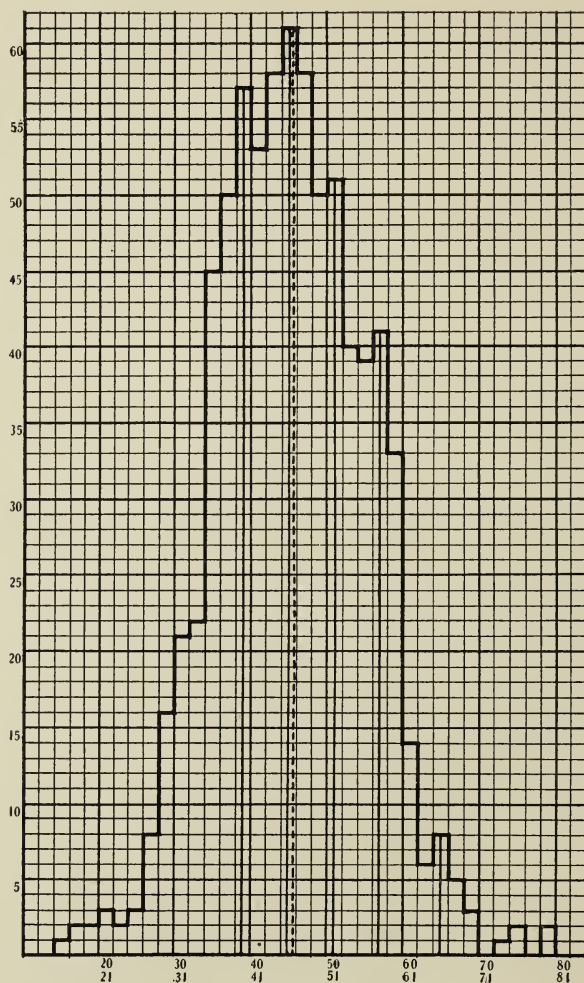


FIG. 10.—Disk-floret curve for 757 heads collected in 1903; classes doubled; mean  $44.933 \pm .238$ ; empirical modes 38-39, 44-45, 50-51, 56-57, 64-65;  $\sigma = 9.703 \pm .168$ .

significance. To make the curve comparable with that offered by the disk-florets in 1900, the classes were doubled, but this still leaves

five prominent modes. The positive skewness is not so marked as in the bracts and rays, but inspection of the curve will show plainly that the theoretical mode is below the mean, though the principal apparent mode nearly coincides with the mean. The standard deviation is  $9.703 \pm .168$  and the coefficient of variability  $21.595 \pm .374$ .

4. *Summation, 1900 and 1903.*—The more important constants for bracts, rays, and disk-florets are given in Tables E, F, and G, along with the corresponding data for 1900 and the summation of the two lots. The summation-curves of bracts, rays, and disk-

TABLE E.  
CONSTANTS OF BRACTS FOR 1900, 1903, AND THEIR SUM.

	1900	1903	Combined
Number.....	658	757	1415
Mean.....	44.044	38.597	41.130
P. E. M.....	$\pm .150$	$\pm .189$	$\pm .131$
Modes, empirical....	$\left\{ \begin{array}{l} 34, 39, \\ 43, 49 \end{array} \right.$	$\left\{ \begin{array}{l} 29-30, 34, \\ 39, 41, 46, \\ 49, 51 \end{array} \right.$	$\left\{ \begin{array}{l} 30, 32, 34, \\ 39, 41, \\ 43, 49 \end{array} \right.$
$\sigma$ .....	5.717	7.692	7.313
P. E. $\sigma$ .....	$\pm .106$	$\pm .133$	$\pm .093$
C. V.....	12.979	19.928	17.775
P. E. v.....	$\pm .241$	$\pm .345$	$\pm .225$

TABLE F.  
CONSTANTS OF RAYS FOR 1900, 1903, AND THEIR SUM.

	1900	1903	Combined
Number.....	658	757	1415
Mean.....	28.038	25.247	26.545
P. E. M.....	$\pm .107$	$\pm .122$	$\pm .086$
Modes, empirical....	27, 31, 33	16, 22, 26, 33	16, 22, 26, 31, 33
$\sigma$ .....	4.070	4.990	4.792
P. E. $\sigma$ .....	$\pm .076$	$\pm .087$	$\pm .061$
C. V.....	14.516	19.764	18.052
P. E. v.....	$\pm .270$	$\pm .344$	$\pm .229$

florets, together with the two partial curves of which each is composed, are shown in *figs. 11, 12, and 13*. These curves are all reduced to the same area, 500 units, in order to facilitate comparison, and the method of "loaded ordinates" is used to allow the curves to be superposed.

The bracts for the two years combined present no less than seven empirical modes, showing without question that 1415 heads is still too few for material having so wide a range and so high standard deviation. In the rays, the range being less and the standard deviation

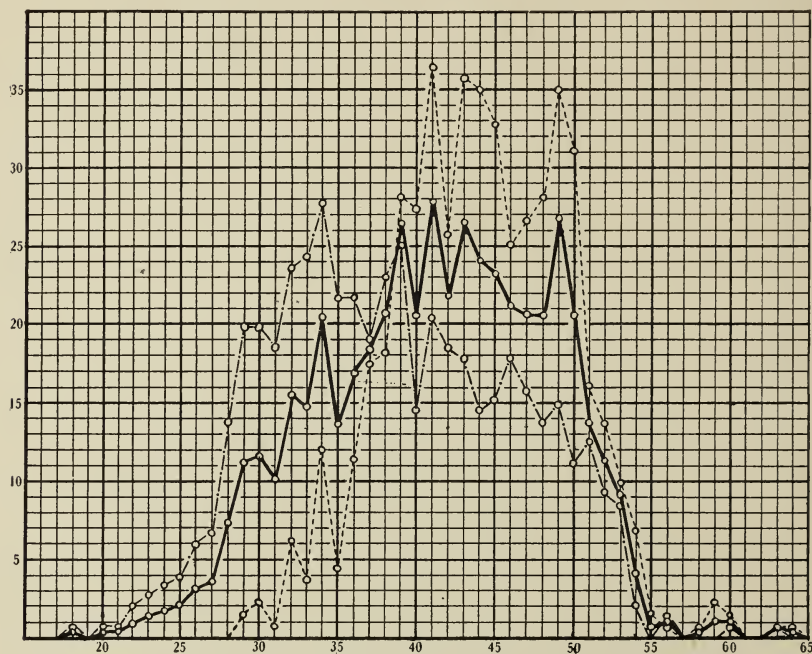


FIG. 11.—Summation curve for bracts 1900+1903 and the bract-curves for 1900 and 1903 superposed for comparison; all reduced to the same area, 500 units; heavy line the summation curve; dotted line the 1900 curve; dot and dash line the 1903 curve.

TABLE G.

CONSTANTS OF DISK-FLORETS FOR 1900, 1903, AND THEIR SUM.

	1900	1903	Combined
Number.....	658	757	1415
Mean.....	50.298	44.933	47.428
P. E. $\mu$ .....	$\pm .166$	$\pm .238$	$\pm .156$
Modes, empirical....	$\left\{ \begin{array}{l} 48-49, \\ 52-53 \end{array} \right.$	$\left\{ \begin{array}{l} 38-39, \\ 44-45, \\ 50-51, \\ 56-57, \\ 64-65 \end{array} \right.$	49-50
$\sigma$ .....	6.310	9.703	8.724
P. E. $\sigma$ .....	$\pm .117$	$\pm .168$	$\pm .111$
C. V.....	12.546	21.595	18.395
P. E. $v$ .....	$\pm .233$	$\pm .374$	$\pm .233$

tion only two-thirds as great, the number of heads is much more nearly adequate. There are presented five empirical modes, 16, 22, 26, 31, 33, almost in agreement with LUDWIG's series.

5. *Correlations.*—The correlation between rays and bracts is shown in *fig. 14*, between rays and disk-florets in *fig. 15*, and between

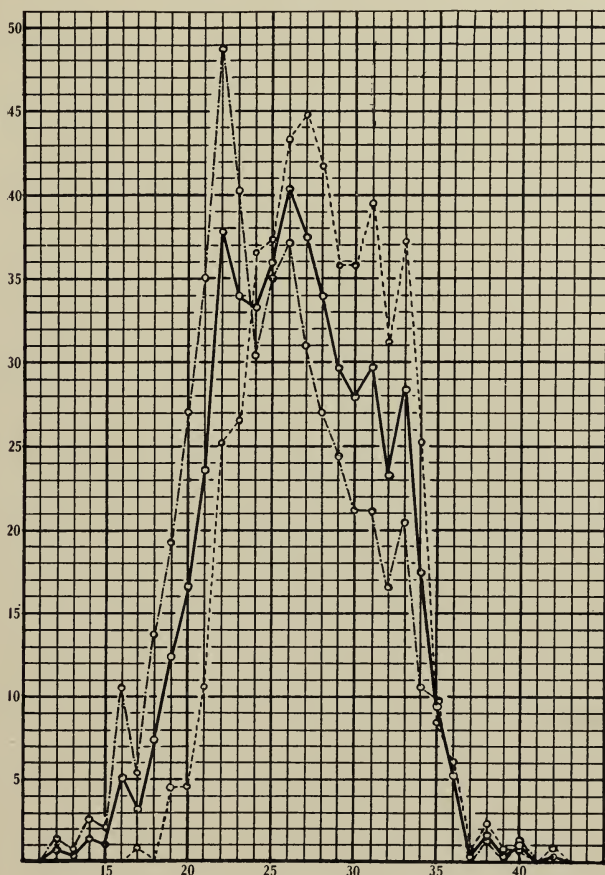


FIG. 12.—Summation curve for rays 1900 + 1903 and the ray-curves for 1900 and 1903 superposed for comparison; all reduced to the same area, 500 units; heavy line the summation curve; dotted line the 1900 curve; dot and dash line the 1903 curve.

bracts and disk-florets in *fig. 16*. The coefficient of correlation is very high in all, being greatest between rays and bracts, and least between rays and disk-florets. The coefficients may be compared with those of 1900 in Table H:



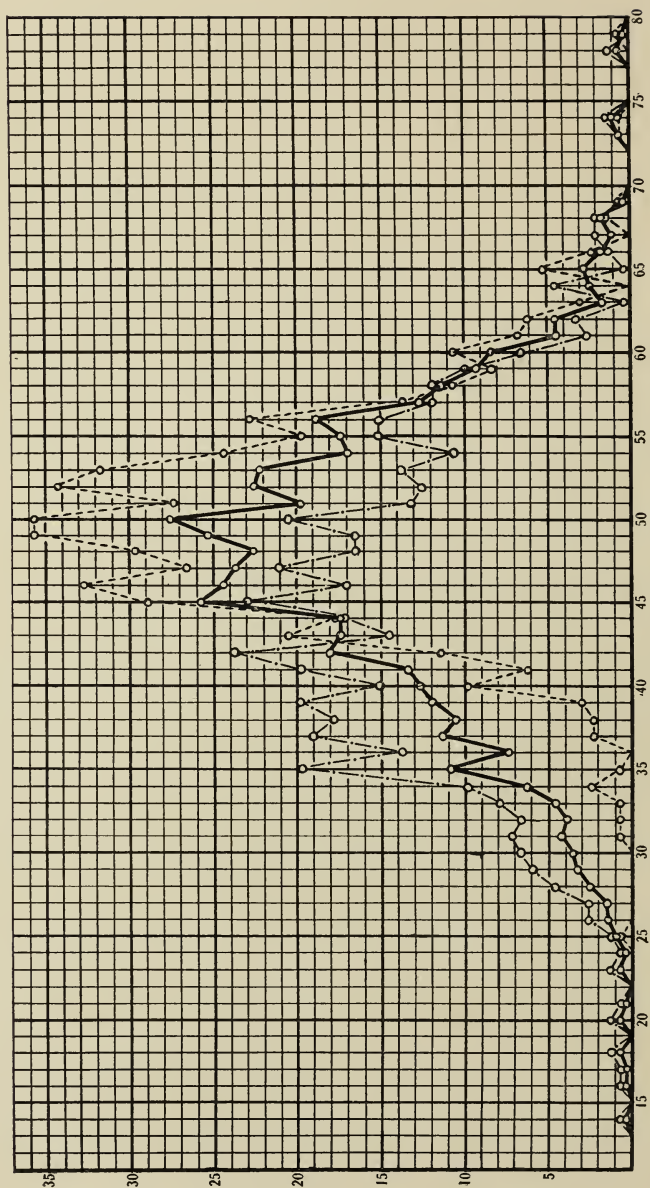


FIG. 13.—Summation curve for disk-florets 1900 + 1903 and the disk-floret curves for 1900 and 1903 superposed for comparison; all reduced to the same area, 500 units; heavy line the summation curve; dotted line the 1900 curve; dot and dash line the 1903 curve.



TABLE H.  
COEFFICIENTS OF CORRELATION.

	1900	1903
Rays and bracts.....	.7051 ± .0092	.8745 ± .0042
Rays and disk-florets.....	.6749 ± .0100	.8240 ± .0058
Bracts and disk-florets.....	.....	.8355 ± .0055

#### V. DISCUSSION.

In my earlier study the conclusion was reached that the mean number of parts in the heads of *Aster prenanthoides* begins high and falls continuously from the beginning to the end of the flowering season. This was recognized as in accord with BURKILL'S (1895) results on *Alsine media* and other species. REINÖHL (1903) has recently made a very careful study of *Alsine media* and reports that the first flowers never have the highest number of stamens and that the maximum number is reached only after some time. He attributes BURKILL'S results to the fact that they were based upon occasional collections which, he supposes, did not happen to involve the very earliest flowers of the season. My collections of *Aster prenanthoides* in 1900 included all the heads which bloomed that year, but the first collection was made so late that the mean numbers of parts in the very earliest heads were indeterminable because of their association with heads of later development; but in 1903 the collections were made with such frequency as more closely to analyze the changes taking place during the season, there being presented here twelve successive collections instead of four.

It is now shown that in *Aster prenanthoides* also the mean numbers begin low, leaping almost immediately to the maximum, and thence falling more gradually till near the end of the season. Inspection of fig. 7 will make it clear that four collections in 1903, made on the same dates as the 1900 collections, would have led to the conclusions then reached that there is a continuous fall from the beginning to the end of the season.

It will be noted in the same figure that the last collection in 1903 shows a rise in mean values. As this collection consisted of but four heads, it can be considered as having little significance. I believe, however, that this condition will be found to occur not infrequently.



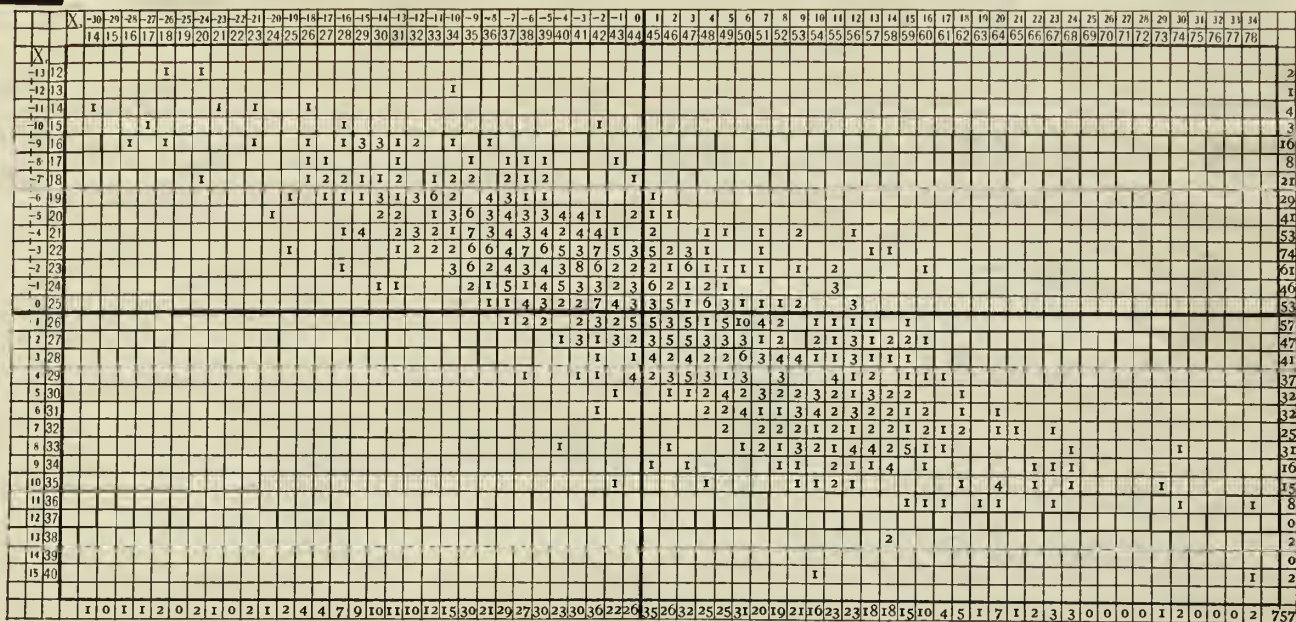


FIG. 15.—Correlation surface for 757 heads collected in 1903; rays subject, disk-florets relative;  $\rho = .8240 \pm .0058$ .

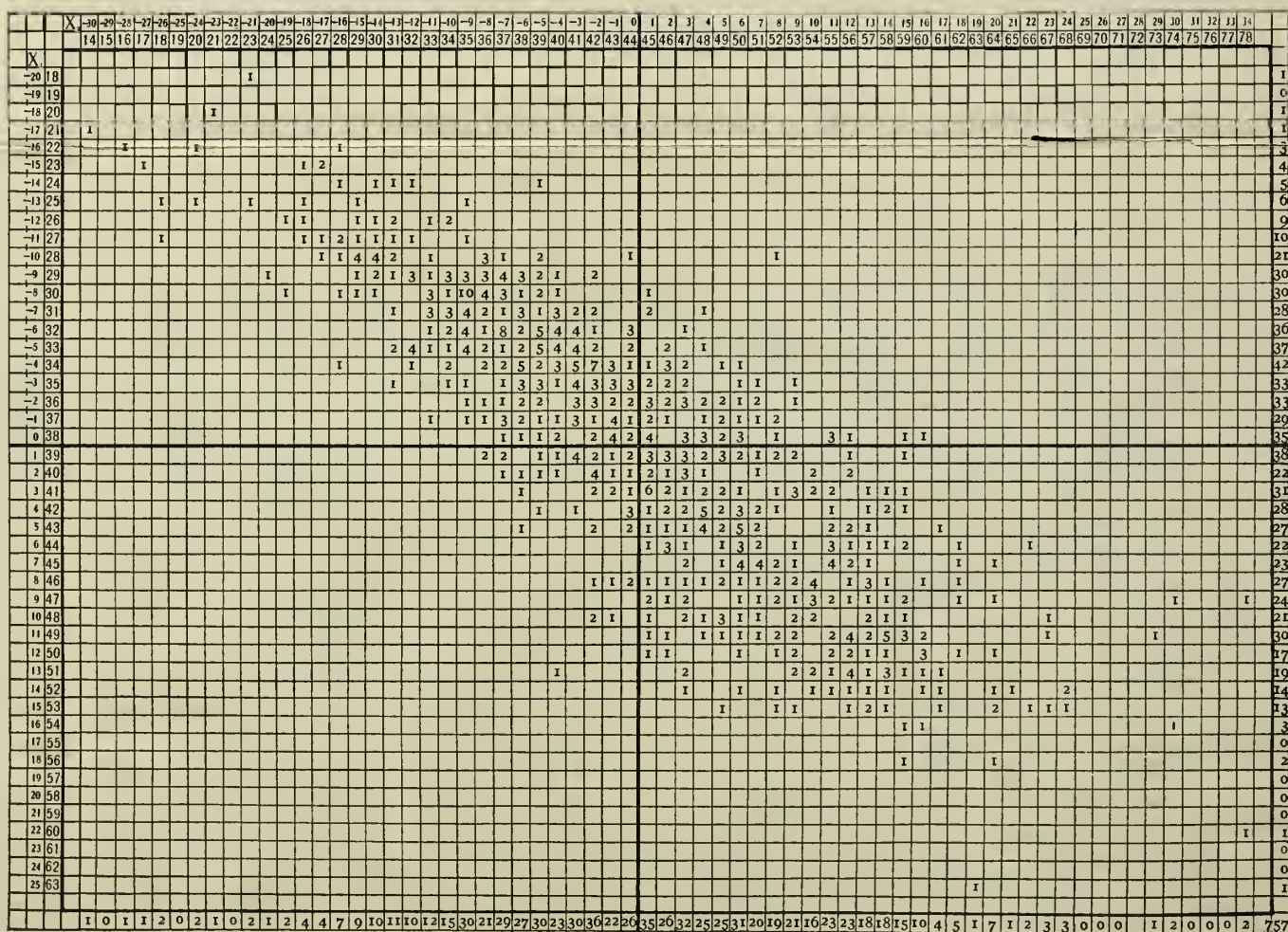
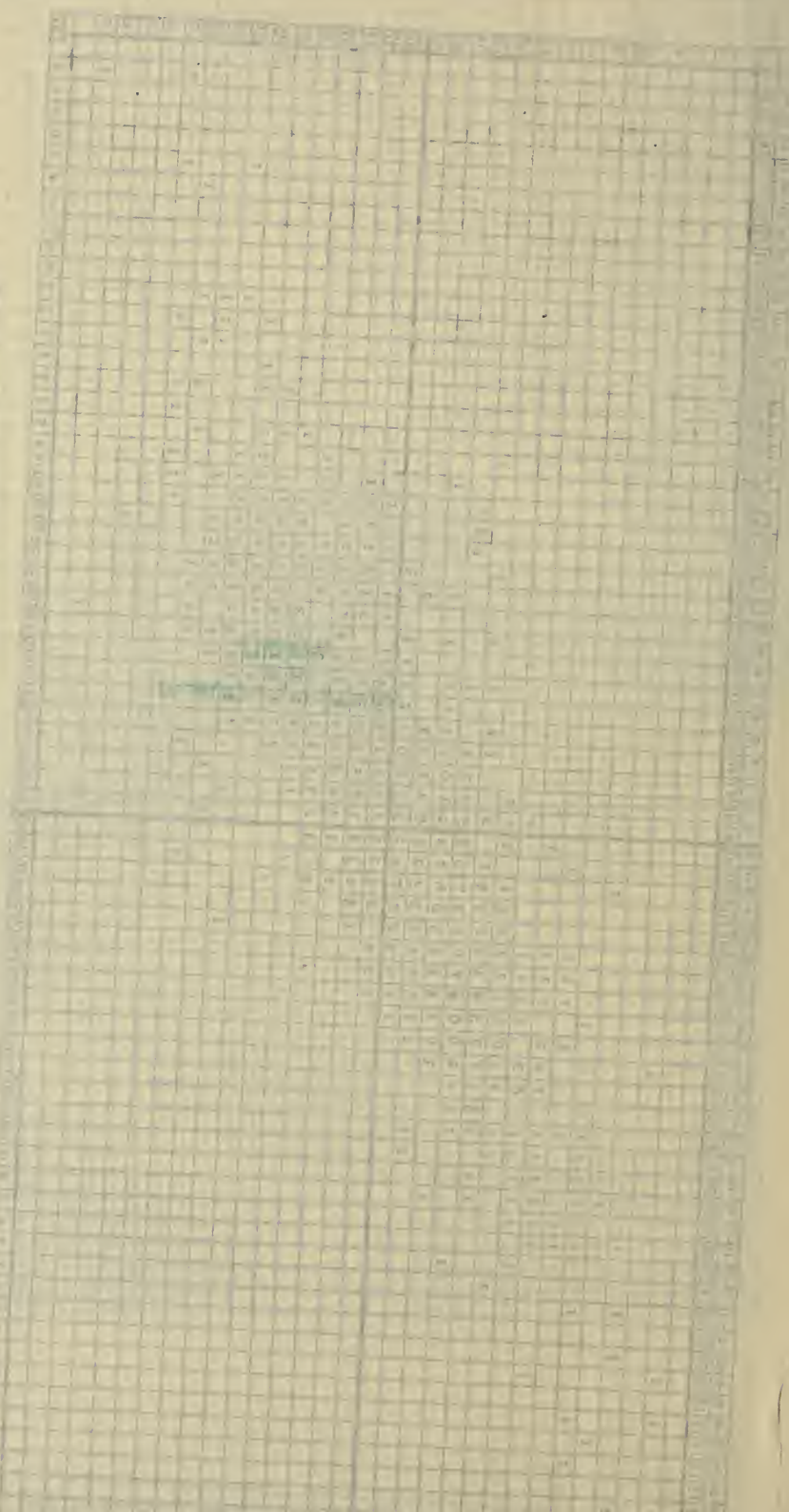


FIG. 16.—Correlation surface for 757 heads collected in 1903; bracts subject, disk-florets relative;  $\rho = .8355 \pm .0055$ .

Figure 1. A grid of 100 squares, each 1 cm by 1 cm, used for measuring the area of a shape. The grid is labeled with numbers 1 to 10 along the top and left edges. A green shape is drawn on the grid, consisting of a 3x3 square with a 1x1 square attached to the right side of the bottom row. The area of the shape is 10 square units.





It was observed by BURKILL (1902) in *Ranunculus arvensis* L., but he did not "feel justified in suggesting a cause for it." BURKILL (1895) showed in his earlier paper that in *Caltha palustris*, *Ranunculus arvensis*, and *R. bulbosus* the first flower of any individual has a higher number of stamens than any subsequent flower of that individual. HAACKE (1896) points out the same fact in regard to the number of rays in the heads of *Tanacetum* (*Chrysanthemum*) *corymbosum*. If this is also true in *Aster prenanthoides* (and I believe it is), how are we to account for the peculiarities of the curves in fig. 7? The general fall in mean values from near the beginning to near the end of the flowering period can be best explained perhaps by the gradual waning of vegetative vigor during the time at which the differentiation takes place which determines the number of parts in the heads. This decreasing vigor was supposed by BURKILL (1895) to be largely due to changing temperature, but REINÖHL (1903) has shown that temperature has little if any influence, while the important factor seems to him to be that of available food-supply. It is conceivable that there may be a decreasing lability of the protoplasm resulting from lessened water-supply, or the accumulation of inert products of metabolism, or from other causes, which would bring about a progressive fall in the number of parts in the heads, even though the food-supply remained unchanged.

But if every individual produces the highest number of parts in the first head that blooms and the lowest number of parts in the last, how can the mean number begin low—far below the maximum—and end with a rise? This is to be explained by the fact that we are dealing with a population instead of an individual. The precocious flowering of starved or otherwise weakened individuals is a well-known phenomenon, and it is evident that the heads gathered at the first collection were those produced by the very weakest individuals, and owe their low values to that fact. Very soon, however, the mediocre plants, composing the great majority of the population, begin to bloom, thus bringing the mean values at once to the maximum, from which they gradually fall until almost the end of the season. The very last to bloom will undoubtedly be the last heads of certain very vigorous individuals which did not begin to bloom till late in the season, and though these heads have the lowest numbers of parts produced

by those individuals, they yet have higher numbers than the last heads of the mediocre portion of the population which determined the minimum mean value. These facts will be made clear by a reference to *fig. 17*, in which the numerous oblique parallel lines represent the change in mean number of parts in the heads of the

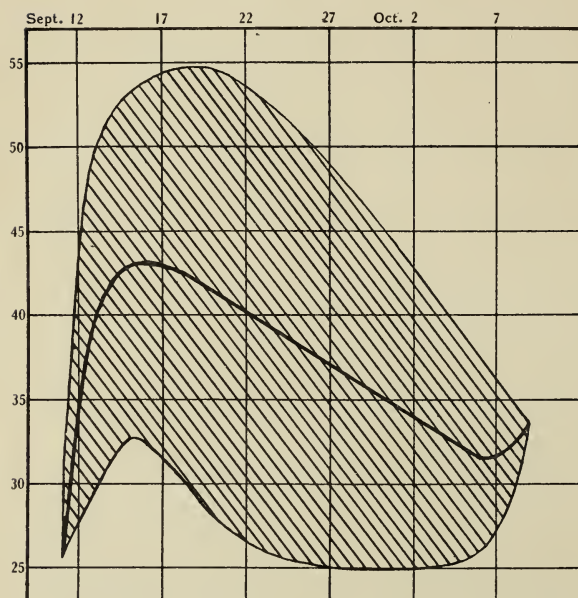


FIG. 17.—Schematized representation of the changes in mean number of parts in the heads of the 1903 population; each of the parallel oblique lines represents the change in a single stem; the heavy line shows the change in mean value for the whole population.

individual stems composing the population. The abscissal distances of the ends of a given line indicate the time at which the individual represented by that line began to bloom and that at which it ceased blooming, while the ordinatal distances of the same points represent the number of parts in the first and last heads produced. The heavy line running through the middle of the figure is the exact mean of the figure as drawn. This figure is somewhat schematic, of course, but it is not wholly imaginary. The

mean is suggested by the 1903 bract-curve of *fig. 7*, and the outline will be recognized in the distribution of numbers in Table A, which also belongs to the bracts of the 1903-population, so that *fig. 17* may be looked upon as a slightly schematized representation of the bracts as they actually occurred in 1903.

In 1900 the change in mean values from the maximum to the minimum was 11.6 per cent. in bracts, 14.4 per cent. in rays, and 18.9 per cent. in disk-florets; and in 1903 it was 24.6 per cent. in bracts, 22.3 per cent. in rays, and 26.4 per cent. in disk-florets. This con-

siderable change in the constants of variable characters during the single season is now generally recognized, as has been made manifest in the discussions which were roused by LUDWIG'S (1901) interpretation of such differences as indicative of the establishment of local races or *petites espèces*. Miss LEE (1902) says in her discussion of LUDWIG'S results and conclusions, "we require in fact to know how the means, variabilities, and correlations of the characters of a plant change (i) with its season and (ii) with the influence of environment before we can formulate a test for racial differences," and PEARSON (1903) and other recent writers make similar statements.

While there is thus a general recognition of the changes which may be expected to take place during a single season, there is still a question as to changes of variability from season to season. This is the first investigation in which factors involved in modifying the variable characters of plants or animals have been so completely limited to the dissimilarity of different seasons. Although a number of students have at times found differences similar to those presented in this paper, their material has been collected nearly always in such a way as to allow of some other interpretation, and the conclusions arrived at have in consequence usually assumed the absence of seasonal fluctuations.

YULE (1902) has investigated the number of sepals of *Anemone nemorosa* growing in several different habitats in the neighborhood of Bookham, Surrey, England, during the years 1889-1900, but unfortunately his collections were not made at coincident dates of the several years, and one of the habitats had changed during the time in which the observations were made from an exposed clearing to a well-grown shady copse. Although he interprets his results as indicating a considerable fluctuation from season to season, his data can be thrown into a single series and shown to exhibit just the changes which recent investigations of REINÖHL (1903) on *Alsine media* and the results recorded here for *Aster prenanthoides* show to occur during a single season. Thus, taking YULE'S data for habitat (C), which he describes as a narrow strip of copse at Little Bookham, and arranging them according to the time of year at which each collection was made, without regard to the year, we have for the mean number of sepals: April 8-12, 1899, 6.63; April 15,

1900, 6.81; April 21-22, 1898, 6.76; May 7, 1898, 6.51. A comparison of these results with the curves in fig. 7 will show them to be strictly comparable with the conditions exhibited by *Aster prenanthoides* in the single season of 1903. They differ, however, in being much less striking, the greatest change of mean value in *Anemone nemorosa* being only 4.4 per cent., while the greatest change in mean value in *Aster prenanthoides* was 26.4 per cent.

The Clifton area of *Aster prenanthoides* is in a perfectly natural condition, and though the region is much visited for its fine scenery, this particular spot, being less attractive to tourists and at the same time more difficult of access, is not likely to be at any time seriously disturbed. It can be assumed with perfect assurance that there were no appreciable differences in the habitat in the two years 1900 and 1903, except such as were due to meteorological differences, and to these factors or possibly to internal periodicity, or a combination of these internal causes and climatic changes must be attributed the great differences found.

It has not been infrequent to find great differences in variable characters of plants from markedly different habitats, as in the daisies (*Chrysanthemum Leucanthemum* and *C. segetum*) collected from barren hills and fertile valleys by LUDWIG and DE VRIES. But here at Clifton, Ohio, in the same spot, in the very same group of plants, undoubtedly consisting largely of the uniparental offspring of the very same individuals, the mean number of bracts was nearly 12.4 per cent. less in 1903 than in 1900, the mean number of rays was nearly 10 per cent. less, and the mean number of disk-florets 10.6 per cent. less.

If such differences as these are due to climatic fluctuations, it is of interest to consider what factors may have been important in producing them. As already mentioned, REINÖHL (1903) considers the chief factor in determining the number of parts in the androecium of *Alsine media* to be the condition of the available food-supply, whether this be dependent upon the character of the soil or upon photosynthetic activity conditioned by the intensity of the light. As the physical and chemical conditions of the soil in the Clifton ravine were doubtless essentially the same in the two years in question, the only soil factor which need be taken into account is water-supply as influenced by precipitation. REINÖHL (1903) states that he could



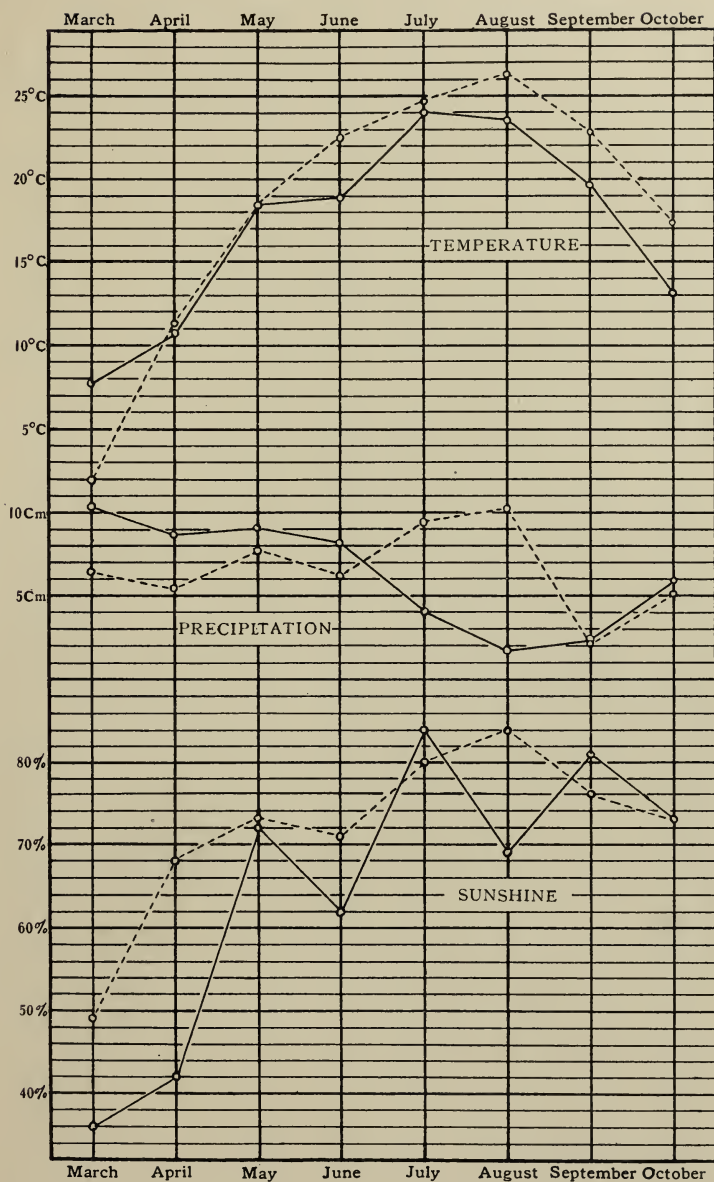


FIG. 18.—Comparison of the climatic conditions during the growing season of 1900 and 1903; dotted lines for 1900; unbroken lines for 1903; temperature curves represent conditions at Dayton, Ohio; precipitation curves are for Cedarville, Ohio; and the sunshine curves for Cincinnati, Ohio.

observe no influence produced by differences of temperature other than that of acceleration or retardation, but as conditions of nutrition are greatly affected by temperature, it is conceivable that it may be in some cases an important factor in determining variability. On these considerations I have sought to compare the season of 1903 with that of 1900 with respect to temperature, precipitation, and light. As the U. S. Weather Bureau records are not complete for any of these factors at Clifton, I have compared the conditions at the nearest stations at which complete records were available. In *fig. 18* these comparisons are represented graphically, the temperature-curves representing conditions at Dayton, Ohio, about 60 <sup>km</sup> distant, the precipitation-curves made from data for Cedarville, Ohio, 10 <sup>km</sup> distant, and the curves for light-intensity from the self-recording instrument at Cincinnati, Ohio, 160 <sup>km</sup> distant. These data are tabulated in Tables I, K, and L, along with the eleven-year or twelve-year normal, and such fragmentary data as were attainable for Clifton itself.

As this is the first attempt to refer changes in the variability of plants in a state of nature to definite climatic changes, there are obvious difficulties in the way of making satisfactory interpretations, and these difficulties can be overcome only by further study. We need to know (*a*) the relative importance of the several factors involved, (*b*) the harmonic optimum of each climatic factor for the species in question, (*c*) whether the critical period is that which precedes or that which accompanies differentiation, (*d*) the time of beginning and ending of the period of differentiation.

TABLE I.  
TEMPERATURE IN DEGREES CENTIGRADE.

	DAYTON, O.			CLIFTON, O.	
	1900	1903	11-yr. normal	1900	1903
March.....	2.0	7.7	4.3	....	8.9
April.....	11.3	10.7	11.3	10.3	10.6
May.....	18.4	18.4	17.4	18.0	17.9
June.....	22.4	18.9	22.6	....	17.9
July.....	24.7	24.0	24.8	24.3	23.0
August.....	26.2	23.5	23.0	25.1	22.6
September.....	22.7	19.7	19.5	....	....
October.....	17.2	13.1	12.6	....	13.1

TABLE K.  
PRECIPITATION IN CENTIMETERS.

	CEDARVILLE, O.			CLIFTON, O.	
	1900	1903	11-yr. normal	1900	1903
March.....	6.45	10.41	10.14	....	7.98
April.....	5.51	8.79	5.87	4.83	8.51
May.....	7.70	9.07	8.71	5.00	11.58
June.....	6.20	8.20	8.18	....	11.94
July.....	9.32	4.11	9.63	13.05	3.05
August.....	10.29	1.75	5.54	9.04	.79
September.....	2.08	2.46	5.74	....	....
October.....	5.11	5.92	4.67	....	5.77

TABLE L.  
LIGHT-INTENSITY AT CINCINNATI, OHIO.

	1900	1903	12-yr. normal
March.....	49%	36%	45%
April.....	68	42	56
May.....	73	72	62
June.....	71	62	72
July.....	80	84	76
August.....	84	69	75
September.....	76	81	72
October.....	73	73	..

No study has been made to determine the period of differentiation in *Aster prenanthoides*, but I am assured by Dr. C. J. CHAMBERLAIN, who has studied *Aster Novae-Angliae*, that some of the heads in that species are already blocked out by the first of July. I consider it a fair assumption that the period of differentiation of the parts of the head in this species lies between June 1 and August 1.

If we accept the normal climatic conditions as near the harmonic optima (and this may not be a very erroneous assumption, since the area in question is near the center of range), we find that the conditions were more favorable in 1900 (*a*) with respect to June and July temperatures, the temperature for these months in 1903 being considerably below normal, (*b*) in July precipitation, 1903 having less than half the normal precipitation for that month, and (*c*) in light-intensity for every month, except possibly May, up to August 1, after which no factor could have any further influence. It may well be a question,

however, whether the harmonic optimum for light-intensity is not likely to be above the normal, the shade habit of *Aster prenanthoides*, as well as of other green shade plants, being assumed on account of the protection afforded against excessive transpiration, and not against excessive lighting. If this be true, the conditions in 1900 were even more favorable than here assumed, since with the exception of July the light-intensity was higher in 1900 than in 1903, being generally above normal in the former year, while in 1903 it was generally much below normal, being strikingly below in April and June.

These several advantages of 1900 over 1903 seem to be offset by the single factor of precipitation during May and June, the rainfall being appreciably below normal during those two months of 1900. As pointed out in the discussion of the habitat, it is probable that precipitation is of very slight importance in this case, leaving the low light-intensity and low temperature of the month of June, 1903, as probably the most important factors in bringing about the great change in the number of parts in the heads, the factors of next importance being possibly the very high light-intensity coupled with slight precipitation in the month of July 1903.

I wish to repeat that these conclusions are based on assumptions which need confirmation. It must not be forgotten that the after-effects of a preceding season or a rigorous winter may also be factors of importance, or even that there may be an internal periodicity which cannot be definitely referred to environmental fluctuations.

Two features of the frequency polygons for the bracts, rays, and disk-florets (*figs. 8-10*) are sufficiently striking to warrant consideration, their multimodality and their skewness. So much has been written upon the multimodal character of the frequency curves of phyllotactic organs that it need only be pointed out here that this additional collection of material shows no tendency to eliminate the multimodality observed in 1900, and though the errors of random sampling, which are very great in material of such wide range, must be held to account for most, if not all, of the irregularities of these curves (PEARSON 1902), there are some evidences that permanent modes may be developed on the Fibonacci series and LUDWIG'S "Unterzählen."

The constant recurrence of this series is not to be taken, however,



as has been maintained by LUDWIG (1899, 1901), as proof that variation in plants is fundamentally different from that in animals. When the phyllotactic series shall have been successfully analyzed, they may be found to result from the working out of more or less definite cell-lineages as supposed by LUDWIG (1888), or they may be the result of purely mechanical relations, as believed by SCHWENDENER, followed by WEISSE (1897) and CHURCH (1904), but either hypothesis, in explaining the occurrence of such series, must leave departures from the theoretical numbers to be accounted for as fluctuating variations. In addition to this variation about each number of the series, there is the general variation which may have a sufficiently wide range to allow the variates to coincide with two or more numbers of the phyllotactic series, so that we have in the case of phyllotactic variants two series of variations, the one overlying and partially masking the other. There can be little doubt that these variations taken separately will be found to agree with all the laws of variation determined for animals and the non-phyllotactic characters of plants.

Although DE VRIES (1899*b*) was able by selection to establish races of *Chrysanthemum segetum* having monomodal ray-curves, this must not be taken as supporting LUDWIG'S (1901) view that multimodality is due to the establishment of a mixed population of *petites espèces* through the common occurrence of asexual and autogamic sexual reproduction, for REINÖHL (1903) was able to reduce the multimodal curves of *Alsine media* to monodal curves *without selection*, by different degrees of light and manuring.

It is to be hoped that we shall soon have a method of treatment of phyllotactic variants which will remove the Fibonacci mask and permit the analysis of the underlying individual variation with as much precision as is now attained with non-phyllotactic variants.

Although it is impossible on account of the multimodality of these curves to analyze the skewness, it is so marked in the case of the bracts and rays (*figs. 8 and 9*) as to be recognized at a glance. There have been various interpretations of skewness in different connections, favorite early views (DAVENPORT 1901) being that it results either by the elimination of one or other of the extremes through the process of natural selection, or that heterogeneity is introduced by the

development of a new race within the range of the old but centering about a different mean. It is also believed that skewness may result from physiological causes having no direct bearing upon the origin or modification of species. While in no specific case may the suggested interpretation be the correct one, these different views may at least be accepted as evidence that skewness may result from various causes, and that it is therefore not self-explanatory.

If the 1903 curves are compared with those for 1900 in *figs. 11-13*, it will be seen that in every case the positive sides of the curves are approximately coincident, but on the negative side there is a very material disagreement. According to the recent discussion of skew variation by LUTZ (1904), we have here a case of skewness produced by the addition of variates, and this addition of such magnitude as already to overtop the 1900 population, thus giving a fine example of "historic" skewness; but no one can be convinced that this is here due to the "starting of a new race about a mean within the range of the old race."

It is evident that the skewness is here the result of direct physiological reaction to the changed environment. Not all individuals are alike sensitive to changed conditions, some being more, some less affected by a given amount of change; so that while many individuals respond to the less favorable conditions by the production of heads with smaller numbers of parts, there is still a considerable number of conservative individuals which are little or not at all affected. The positive skewness of these curves is due to the fact that only a small proportion of the population is conservative. If the great mass of variates had been comparatively conservative and only a small percentage sensitive to the changed conditions, it is plain that the position of the principal modes would have been little affected, while the mean would have been lowered and negative skewness would have been the result. This would then have been a case of so-called "prophetic" skewness. We may say then that in cases of direct or physiological variation, prophetic skewness indicates slight sensitiveness, and historic skewness great sensitiveness,<sup>5</sup> to the changed conditions, provided always, of course, that under ordinary conditions the distribution of the variates affected is normal.

<sup>5</sup> As measured by the number of sensitive individuals, not by the degree of sensitiveness of each individual.

Cases are well known in which the distribution does not appear to be normal under any ordinary conditions, the frequency curves being of the "half Galton" type, as for instance the petals of *Caltha palustris*, *Potentilla anserina*, *Ranunculus bulbosus* (DE VRIES 1894), *Ranunculus repens* (PLEDGE 1897), sepals and petals of *Ranunculus arvensis* (BURKILL 1902), leaflets of clover (DE VRIES 1899a), ascidia and other abnormalities of various species (DE VRIES 1899a, TAMMES 1903), and other characters. Such cases may not be really so exceptional, however, as they at first appear. We have only to assume that the normal condition for these characters is one in which the value of  $\sigma$  approaches zero to see that these are cases of "prophetic" skewness due to the small proportion of abmodal variates; in other words, due to slight sensitiveness to conditions tending to produce a number of organs higher or lower than the normal mode.

It may be found that any population or even any species is sufficiently uniform in its reactions to various degrees of environmental change to allow us to derive from the direction and amount of skewness the approximate value of the mean under average conditions or under conditions which would give a normal distribution of the variates. Thus, the knowledge that this population of *Aster prenanthoides* is so sensitive to change as to exhibit strong positive skewness when conditions are below average may be found to warrant the assumption that there will be a strong negative skewness under unusually favorable conditions, and also that the skewness exhibited by a collection from any new locality would give an indication by its direction as to whether that collection was below or above the average prevailing condition for that place. But before we can apply this principle with any confidence in determining the "normal mean" of any particular population, it will be necessary to confirm our assumptions (a) that the distribution for that population is normal under average conditions, and (b) that the sensitiveness to unusually favorable conditions is similar in intensity to the sensitiveness to unfavorable conditions.

The principle here presented of variability in individual sensitiveness to changes of environment is likely to find a wide applicability in the interpretation of skew variation, and suggests the need of first determining whether or not there is direct variation of the organ or

character under consideration before assuming that either natural selection or mutation is involved in any given case of skewness. And although this is most strikingly true of plants, it must likewise be true of animals, especially of animals having a short life-cycle, so that no investigation can be considered as giving satisfactory support to any hypothesis of evolution until the sensitiveness of the character under consideration to secular changes shall have been determined.

Perhaps even more remarkable than the skewness and the changes in mean value, which have resulted from the less favorable conditions in 1903, is the great increase in value of the coefficient of variability. Reference to Tables E, F, and G will show that the variability in the bracts in 1900 was  $12.979 \pm .241$ , as compared with  $19.928 \pm .345$  in 1903. Corresponding changes are shown in rays and disk-florets, from  $14.516 \pm .270$  to  $19.766 \pm .343$ , and from  $12.546 \pm .233$  to  $21.595 \pm .374$ , respectively. As it has been assumed that the low mean values indicate that conditions were less favorable in 1903 than in 1900, we may accept these changes in the coefficients of variability as proof of the hypothesis that when organisms are introduced into unusual surroundings or subjected to unusual conditions they become more variable, and that this would be favorable to any selective process which might set in as a result of the change. Before too great stress is laid on this conclusion, however, we need to consider the nature of the coefficient of variability. The importance of this constant lies in the fact that it is an abstract number and therefore allows us to compare the variability in characters of different magnitude or even of different quality, as color, form, size, weight, number, etc. It consists of two factors, the standard deviation ( $\sigma$ ) and the mean ( $M$ ), and is expressed by the formula  $C. V. = \frac{100 \sigma}{M}$ . The value of the coefficient of variability will change directly with changes of  $\sigma$  and inversely with changes of the mean. Turning now to the cause of the greatly increased coefficient of variability, we find upon inspecting Tables E, F, and G that the value of  $\sigma$  was in every case considerably higher in 1903 than in 1900, and at the same time that the mean was much lower, so that both factors acted together in producing the high values of the coefficient of variability.

To show that this coefficient is not always a satisfactory measure



of variability, let us assume that conditions had been unusually favorable to such a degree as to give curves with the same values of  $\sigma$ , but negatively skew. The variability would then be approximately the same, but, instead of the coefficient being the same or even nearly the same, it would be very much less, owing to the greatly increased value of the mean. I do not think that  $\frac{100\sigma}{M}$  gives a proper value of the coefficient of variability in cases of skew variation, since its values in positively skew curves are not comparable with those in curves of the same species or even of the same population, which are negatively skew. If the "normal mean" could be derived from skew curves, that might be used instead of the mean in the formula for the coefficient of variability, thus making the value of  $\sigma$  alone indicate the changes of variability from time to time within one and the same population. This would be theoretically correct, but it must be evident that the experimental determination of the normal mean, except through a long series of investigations upon any population under consideration, is impossible, even though, as pointed out above, the degree and direction of skewness may in some cases give a rough approximation to it when the sensitiveness of the species in question is known.

Returning now to the question as to the increased variability due to changed environmental conditions, we find that the present imperfect coefficient of variability, which would tend to minimize the variability when conditions are unusually favorable, would still be considerably increased by such unusually favorable conditions as would result in a negative skewness equal in magnitude to the positive skewness of the 1903 curves. We may confidently accept the results of this study as proof, therefore, that changes of environment do result in increased variability.

It was noted in 1900 that the correlations between the parts in the head were very high, and by reference to Table H it will be seen that in 1903 they were very considerably higher still, the highest coefficient in both years being that between bracts and rays. The exact meaning of changes in the degree of organic correlation is proving a somewhat puzzling problem at the present time. LUDWIG (1901) presents a striking case of this kind as evidence of racial distinctness between

two populations of *Ranunculus ficaria*, but MACLEOD (1899) has shown that similar changes may be found in that species at different times in a single season. I have also found (SHULL 1902) that the coefficients of correlation in *Aster prenanthoides* may be very different at different parts of the season.

Before the significance of such changes can be understood it will be necessary to investigate the nature of correlation when considered in this statistical way. Some biologists use the term "correlation" to designate a relation between two organs or characters, such that the development of the one determines that of the other, as for instance the dependence of the secondary sexual characters upon the primary in animals, or the relation of the internodes to the leaves in plants. In this kind of correlation the failure of the one organ or character to develop, or its removal at an early stage of development, invariably prevents or modifies the development of the other. Every degree of correlation in this sense is found in different cases, and it probably exists to some extent even between organs whose immediate relations to each other are little understood. It is only rarely, however, that this kind of correlation is not insignificant as compared with biometrical correlation. Thus, in the biometrical sense there is a very high correlation between the index fingers of the right and left hands, but the removal of one of these would have no appreciable effect upon the development of the other.

For convenience we may speak of "immediate" or "direct" correlation when one organ or character stands in a direct causal relation to another, and "mediate" or "indirect" correlation in cases of correlated variation in which no such direct dependence exists. Statistical measures of correlation make no distinction between these two kinds of correlation, but as a notable degree of immediate correlation is comparatively rare, while mediate correlation is almost universal, the correlation of parts as spoken of by the biometrician may be considered as mediate or indirect. Mediate correlation between two organs or characters may be defined, then, as their mutual relation to the combination of common causes, such as heredity, nutrition, etc., which determine their quantitative relations. It is the relation which results in proportion and symmetry. When mediate correlation is perfect, *i. e.*, when  $\rho = 1$ , the two organs or

characters are proportionately influenced by every variation in the factors which determine their size, number, or other quantitative relation, and neither is affected by any factor which does not affect the other. The organs do not modify each other, but both are affected by the same conditions. Only confusion results from the failure to appreciate the difference between immediate and mediate correlation, as may be seen in BURKILL'S (1902) discussion of the correlation in the parts of the flower of *Ranunculus arvensis*, when he says that "reduction in the number of petals does not act as a reflex on the number of sepals in anything like the way in which the reduction of sepals may be said to promote reduction of petals."

If as the values of any pair of mediately correlated organs or characters are increased or decreased the correlation between them is changed, it must mean that one or other of them becomes proportionately less sensitive to the causes producing the change of values, and becomes more fixed or more variable in its quantitative relations. Such a change is well illustrated by an interesting diagram presented by BURKILL (1902), in which it is shown that sepals, petals, stamens, and carpels of *Ranunculus arvensis* vary together, *i. e.*, are closely correlated, in flowers having the total number of parts less than 19, but in flowers having a higher total number of parts the sepals become fixed in number at 5, and the correlation between sepals and the parts which continue to increase becomes zero. In flowers with more than 22 parts the mean number of petals likewise becomes fixed at 5. In flowers of still higher numbers of parts the carpels show a tendency to respond with proportionately less increase as compared with the stamens. It is plain then that in this species any conditions which promote the formation of flowers with a high number of parts will tend to decrease the degree of correlation and *vice versa*.

But it is an important fact which must not be overlooked that changes in the *coefficient* of correlation do not necessarily mean an actual change in correlation. PEARSON (1903) has pointed out that heterogeneity in a population tends to increase the coefficient of correlation, but of course such heterogeneity does not increase the actual degree of correlation. It is probable that most of the marked changes which have thus far been observed in coefficients of correla-

tion are to be accounted for in this way. I have already shown that my first collection in 1900 was made long after the beginning of the flowering season, and hence had the earliest heads with low numbers of parts associated with the heads having the highest numbers of parts produced during the season, and this fact sufficiently explains the high correlations found in that collection. A similar explanation may account for the considerable increase in the coefficients of correlation between the parts of the heads in 1903 as compared with those of 1900, as there are associated in the 1903 collection the heads of conservative individuals and those of individuals which were much modified because of their great sensitiveness to the unfavorable conditions in the latter year. It is apparent, therefore, that in cases of changed coefficients of correlation, as in other cases, it is necessary to scrutinize carefully the influence of more or less artificial conditions upon the value of the constants before we can appreciate their biological significance.

The results of this study have fully borne out the suggestion that considerable differences may occur in individual variation from year to year, and it shows that such differences may be even greater than one would expect. It is not likely that this is an extreme case, nor that the differences between these two collections is even near the limit for this species. To some these results may seem to preclude the possibility of deriving anything of further value from quantitative studies of variation, while to others many new problems of great interest and importance will be suggested. The interpretations which students have based upon the assumption that seasonal fluctuations do not occur will have to be greatly revised or discarded altogether, and before we can appreciate the exact bearing of any case of variation upon the great problems of evolution it will be necessary to know the laws governing that variation. It is to problems of this nature that students must direct their earnest attention if we are ever to have a basis for the appreciation of the bearing of individual variation.

#### VI. SUMMARY.

A second collection of heads of *Aster prenanthoides* Muhl. was made in 1903 from the same area at Clifton, Ohio, that supplied material for a quantitative study in 1900. The bracts, rays, and



disk-florets were studied quantitatively, and the results compared with those of the earlier study.

Twelve successive collections were made from the same plot, and it was found that the earliest collection had low mean numbers, that the mean values then leaped quickly to a maximum, falling gradually to near the end of the season, and that the last collection exhibited a rise, the rise in mean values at the beginning and at the end of the season being in disagreement with the conclusion reached in my earlier study. In general, the first head to bloom on any stem has the highest number of parts possessed by any head produced by that stem, and the last to bloom has the lowest number. The low mean numbers at the beginning of the season are due to the precocious flowering of the weakest individuals, and similarly the rise at the end of the season is due to the belated flowering of a few very vigorous individuals.

Comparison of the results with those of 1900 show that the mean values in 1903 were 10-12 per cent. lower than in 1900, and that accompanying these low mean values there are a strong positive skewing of the curves, a remarkable rise in the coefficient of variability, and a considerable increase in the coefficient of correlation.

The difference in the mean values for the two years is attributed to less favorable climatic conditions in 1903, chiefly to low temperature and low light-intensity in the month of June.

The skewness is due to the unequal sensitiveness of individuals to changes of environment. It is positive because the proportion of conservative individuals is small. In direct or physiological variation, "historic" skewness indicates great sensitiveness and "prophetic" skewness indicates slight sensitiveness to the changes of environment.

The great increase in the coefficient of variability is due to an increase in the standard deviation and a decrease of the mean. The present coefficient of variability is not satisfactory in cases of skew variation, and the value of  $\sigma$  alone should be used as the measure of changes of variability in one and the same population.

Changes in the coefficient of correlation may be due either to an actual change of correlation or to the introduction of a greater or less degree of heterogeneity. The latter is probably responsible for the changes noted in this species.

I gratefully acknowledge my indebtedness to Dr. C. B. DAVENPORT, under the inspiration of whose lectures this study was undertaken and under whose direction it was largely carried on; to Miss OLIVE D. COE for the care with which the material was collected, for the negatives from which *figs. 1, 4, and 5* were reproduced, and for the original of *fig. 6*; to the Directors of the U. S. Weather Bureau stations at Columbus, Ohio, and at Cincinnati, Ohio, for climatological data; and to the curators of numerous public and private herbaria for the data upon which *fig. 3* is based.

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